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The Evolutionary Ecology of Plants

EDITED BY

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THE EVOLUTIONARY BREAKDOWN OF HETEROSTYLY

Spencer C. H. Barrett

INTRODUCTION

The mating system is of prime importance for understanding the process of natural selection since it governs the character of genetic transmission and plays a central role in regulating the genetic structure of populations. Flowering plants display a great diversity of reproductive methods, often among closely related taxa. The variation provides suitable experimental material for population biologists interested in testing hypotheses about the evolution and adaptive significance of different mating systems. Among flowering plant families the shift from obligate outbreeding, enforced by self-incompatibility, to predominant self-fertilization is one of the major pathways of mating system evolution (Stebbins 1957, 1974; Baker, 1959a; Jain, 1976). This change in mating pattern has important systematic and ecological consequences since the evolution of selfing often initiates reproductive isolation and speciation (Baker, 1961; Barrett, 1989).

Since Darwin's original work (Darwin, 1877), heteromorphic incompatibility systems (distyly and tristly, Fig. 1) have provided a rich source of material for mating system studies. This is because the genetic modifications affecting mating behavior are often simple, the direction of change readily interpretable and alterations in the floral polymorphisms can usually be observed without difficulty under field conditions. Modifications of heterostylous systems include the replacement of one type of outcrossing system by another such as the evolution of dioecism from distyly and the origin of distyly from tristly. (see Ganders, 1979; Barrett, 1988a for reviews). More frequently, however, heterostylous systems break down in the direction of increased self-fertilization with the commonest pathway being the formation of self-compatible homostyles (Ernst, 1955; Baker, 1959b, 1966). Plants in these groups usually possess anthers and stigmas at the same relative position within a flower and as a result are largely autogamous (Fig. 2 d,e). Many heterostylous genera contain homostylous taxa that are small-flowered, highly self-pollinating, depauperate in isozyme variation, and adapted to

HETEROSTYLOUS GENETIC POLYMORPHISMS

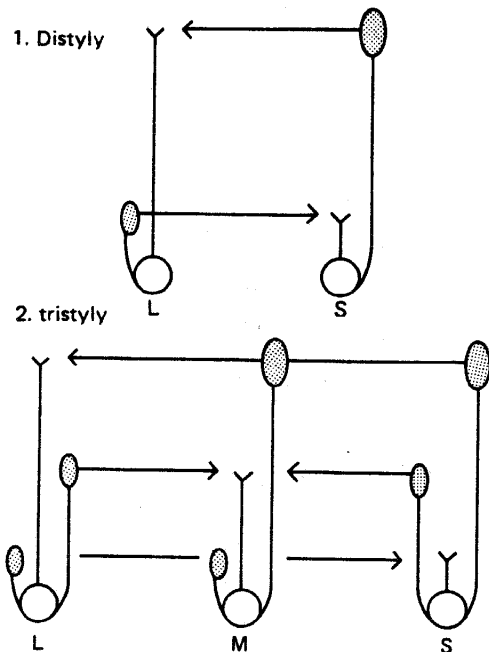


Figure 1. The heterostylous genetic polymorphisms distyly and tristily. Distyly is controlled by a single locus with two alleles. The L morph is usually of genotype ss and the S morph Ss . In tristily the most common mode of inheritance involves two diallelic loci (S and M) with S epistatic to M . With this genetic control the genotypes for the three morphs are: L: $ssmm$; M: $ssMm$; $ssMM$; S: $SsMm$, $Ssmm$, $SsMM$.

pioneer environments. This suggests that the shift to self-fertilization has evolved repeatedly in association with the colonization of temporary habitats. Removed from their normal pollinators and in small newly founded populations, homostylous variants would be favored over outcrossing morphs as a result of fertility selection (Baker, 1955, 1959). My own studies on two heterostylous groups, both of which are composed primarily of colonizing taxa, provide evidence in support of the role of reproductive assurance as a selective factor favoring the evolution of self-fertilization. This chapter reviews work on the evolutionary breakdown of distyly and tristily, respectively, in the *Turnera ulmifolia* complex and in the genus *Eichhornia*. Both

taxa are primarily Neotropical in distribution and the breakdown of heterostyly is associated with the colonization of geographically marginal areas.

HOMOSTYLE EVOLUTION IN THE *TURNERA ULMIFOLIA* COMPLEX

Turnera ulmifolia is a polymorphic complex of perennial weeds composed of diploid, tetraploid and hexaploid varieties (Shore and Barrett, 1985a). Diploid and tetraploid populations are distylous with strong self-incompatibility and a 1:1 ratio of the long- and short-styled (hereafter L and S) morphs in populations (Barrett, 1978). Dimorphism is controlled by a single gene "locus" with L plants of genotype ss and $ssss$ and S plants of genotype Ss and $Ssss$ in diploids and tetraploids, respectively (Shore and Barrett, 1985b, 1987). In contrast, hexaploid populations are homostylous and self-compatible. Homostyles are atypical in possessing wide variation in the relative positions of reproductive organs and hence the facility for autogamy (Fig. 2 c,d,e). The three homostylous varieties that we have studied experimentally are differentiated for morphological traits and isozyme patterns as well as being intersterile. They occur at different margins of the Neotropical range of the species complex (Argentina, Mexico, Caribbean), indicating that distyly has broken down to homostyly on at least three occasions in the complex in association with the hexaploid condition (Barrett and Shore, 1987).

Patterns of floral variation in *T. ulmifolia* are particularly complex in the Caribbean region. On large islands (e.g. Greater Antilles) populations are either tetraploid and distylous or hexaploid and homostylous, whereas on smaller islands (e.g. Bahamas) only homostyles occur. It seems likely that this distribution pattern results from cycles of island colonization and extinction. Homostyles would be favored over the self-incompatible morphs because of the capacity of single individuals to found populations (Baker, 1955; Cox, this volume). On Jamaica, populations are uniformly hexaploid and self-compatible but display a wide range of floral variation from the long homostylous phenotype (long stamens and long styles) to plants with flowers that resemble those of the typical L morph from distylous populations (Fig. 2 c,d). This variation in stigma-anther separation (herkogamy) occurs both within and among Jamaican populations and has an important influence on both the facility for spontaneous self-pollination and the outcrossing rate of maternal parents (Barrett and Shore, 1987). Individuals with well developed herkogamy experience less self-fertilization than

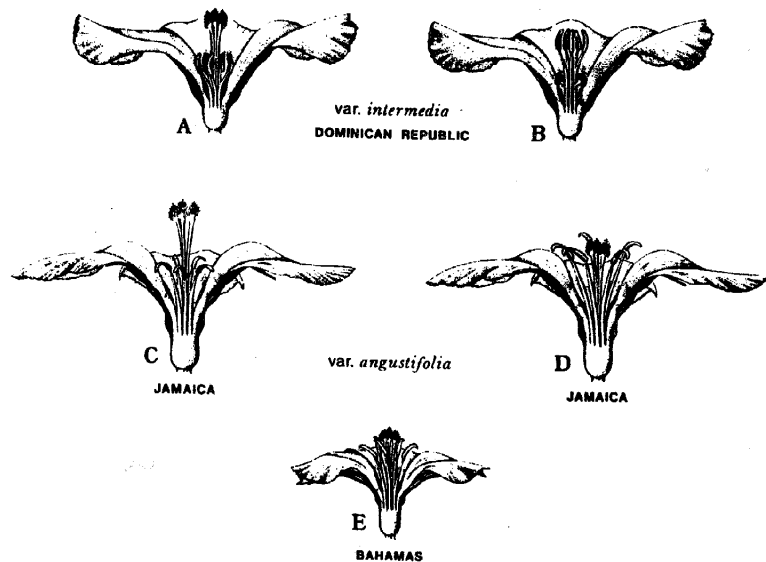


Figure 2. Floral variation in the *Turnera ulmifolia* complex. A,B) L and S morphs, respectively, of *var. intermedia* (4x) from distylous population from the Dominican Republic. C,D) Long homostyles of *var. angustifolia* (6x) from Jamaica with contrasting stigma-anther separations (herkogamy). E) Small flowered autogamous long homostyle of *var. angustifolia* from the Bahamas. After Barrett and Shore (1987).

those in which stigmas and anthers are positioned close together within a flower. The range of floral variation in *T. ulmifolia* raises questions concerning the origin and evolutionary relationships among forms within the complex. In particular, because of the atypical nature of homostyles it is pertinent to ask whether all monomorphic populations in the complex are derived from distylous ancestors as a result of crossing-over within the heterostyly supergene. An alternative possibility is that some phenotypes have originated from L plants through mutation at the SI locus. Mutations of this type occur frequently in the floral morphs of heterostylous species and have been reported in both diploid and tetraploid populations of *T. ulmifolia* (Shore and Barrett, 1986).

It is possible to distinguish between the two alternative hypotheses to account for the origin of homostylous forms in *T. ulmifolia* by assessing the fertility of controlled crosses between

distylous and homostylous plants (Dowrick, 1956; Baker, 1975). If floral monomorphism has arisen by crossing-over within the distyly supergene, residual self-incompatibility in crosses with the L and S morphs is likely to be evident in the pistils and pollen of homostylous plants, irrespective of their relative stamen and style lengths. In contrast, if homostyles with well developed herkogamy are simply L plants that have lost self-incompatibility through mutation, then residual self-incompatibility reactions should be absent in crosses with the distylous morphs.

A crossing program between the distylous morphs and plants from 12 populations comprised of three hexaploid varieties of *T. ulmifolia* were used to distinguish between these two hypotheses (Barrett and Shore, 1987). The results provided clear evidence that the three hexaploid varieties are long homostyles, since the predicted seed set patterns from the cross-over model were revealed in all phenotypes (Fig. 3). Pollen of the S morph was compatible in crosses with homostyles, whereas pollen from the L morph was not. In reciprocals, pollen of homostyles was only compatible in crosses with the L morph. Although some homostylous populations possess "short-level" stamens, their pollen exhibits the incompatibility reaction of long-level stamens of the S morph. Formal genetic analysis of the homostyles also confirmed that they are long homostyles that have arisen through recombination in the distyly supergene (Shore and Barrett, 1985b). The finding that each homostylous variety in *T. ulmifolia* is a long-homostyle provides empirical support for Charlesworth and Charlesworth's theoretical model (1979a) of the breakdown of distyly. They demonstrated that if the "allele" determining the S morph is dominant, as in *T. ulmifolia*, long-homostyles will spread to fixation with greater probability than other self-compatible recombinant phenotypes.

Following each independent origin of long homostyly in the *T. ulmifolia* complex, homostyles colonized habitats not occupied by their distylous progenitors at the margins of the range of the species complex. In some populations it appears that selection pressures favoring increased outcrossing has resulted in the re-establishment of herkogamy. This may be more readily achieved in *T. ulmifolia* through selection on polygenic variation for reproductive organ length than by the *de novo* development of alternative outcrossing systems based on self-incompatibility or dioecism. It is remarkable that despite the shift to hexaploidy and considerable morphological and genetic divergence from their distylous ancestors, homostylous forms in *T. ulmifolia* still retain their ancestral incompatibility behavior, although it serves no apparent function and cannot influence the mating patterns of

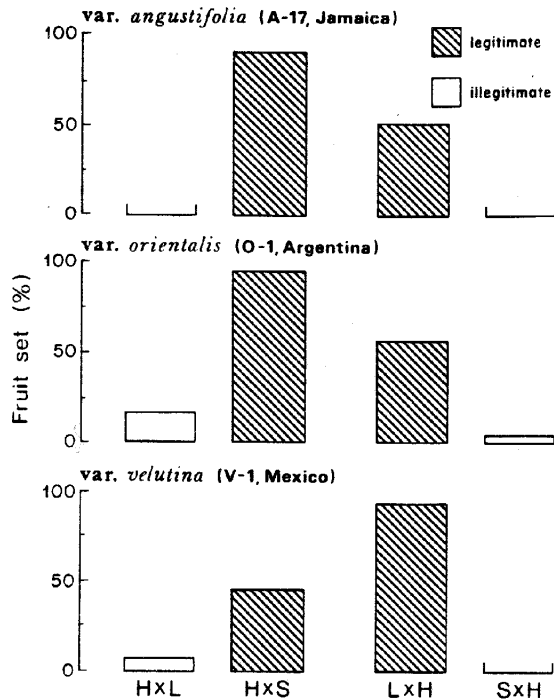


Figure 3. Compatibility relationships between distylous and homostylous varieties within the *Turnera ulmifolia* complex. Histograms illustrate the percentage fruit obtained in crosses between the long- and short-styled morphs (L, S, respectively) and three homostylous (H) varieties. In a distylous population, legitimate crosses are compatible whereas illegitimate crosses are incompatible. For further details see Barrett and Shore (1987).

these self-compatible plants. The evolutionary lability of mating systems in the *T. ulmifolia* complex illustrated in Figure 4 suggests that the evolution of selfing from outcrossing is not necessarily a unidirectional change as has been frequently postulated in other plant groups.

In *Primula* (Ernst, 1955), *Armeria* (Baker, 1966), *Linum* (Baker, 1975), and *Turnera*, the breakdown of dimorphic incompatibility is the result of recombination in the supergene that controls distyly. However, this is not the only genetic mechanism by which incompatibility can be modified in heterostylous groups. A number of taxa are known in which the

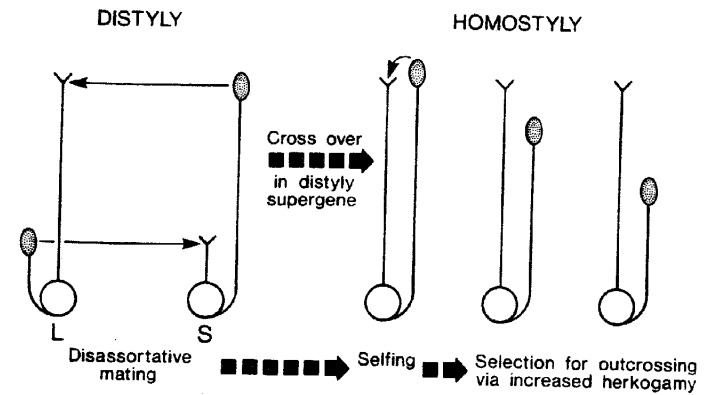


Figure 4. Model of the evolutionary relationships among distylous and homostylous forms in the *Turnera ulmifolia* complex. After Barrett and Shore (1987).

style morphs are highly self-compatible but the stamen-style polymorphism is unmodified. Since it is unlikely that heterostyly can evolve prior to the development of an incompatibility system (Charlesworth and Charlesworth, 1979b; but see Lloyd and Webb, 1989) for an alternative view) it seems more probable that these taxa have secondarily lost their incompatibility systems through the accumulation of self-compatibility mutations at the incompatibility locus. The occurrence of populations of heterostylous species that maintain significant genetic variation for incompatibility expression (e.g., Barrett and Anderson, 1985) supports this view.

SEMI-HOMOSTYLE EVOLUTION IN EICHHORNIA

Among the three tristylous families (Lythraceae, Oxalidaceae and Pontederiaceae) there is good evidence of the repeated breakdown of trimorphic incompatibility to give rise to predominantly self-fertilizing populations (Charlesworth, 1979; Barrett, 1988a). The commonest pathway involves relaxation and eventual loss of the incompatibility system followed by modifications in the relative position of style and stamen heights. The resulting phenotypes, known as semi-homostyles, have one set of anthers adjacent to the stigma and, as a result, are largely self-pollinating. In contrast to the distylous groups discussed above, where a quantum change in incompatibility system and mating behavior occurs through recombination, semi-homostyle

formation in tristylous species usually develops in stages with the mating system evolving gradually towards increased levels of self-fertilization. The evolutionary breakdown of tristily is particularly evident in *Eichhornia*, a small monocotyledonous genus of freshwater aquatics that inhabit Neotropical lakes, marshes, and seasonal pools. Our studies of this group have attempted to integrate information from ecology, genetics, and development in an effort to understand the processes responsible for the repeated breakdown of this complex genetic polymorphism (Barrett, 1988b). Since, with the exception of the notorious aquatic weed, *E. crassipes* (water hyacinth), the group is poorly known, much of our early work attempted to document the taxonomic distribution of breeding systems and chromosome numbers in the genus, and to determine the geographical distribution and ecological preferences of individual taxa. This information has been used to interpret both the phylogenetic relationships and biogeographical history of the group (Eckenwalder and Barrett, 1986).

Of the eight species of *Eichhornia*, three possess large showy flowers and are primarily tristylous, and the remaining five are small-flowered and largely self-pollinating. The selfers exhibit phenotypes which suggest that they are semi-homostylous derivatives of tristylous ancestors. Evidence to support this interpretation is based on the occurrence in populations of the semi-homostylous taxa, of segregation of residual tristylous characters involving weak heteromorphisms of pollen size, style length, and style coloration. Studies of each tristylous species have revealed that floral trimorphism has become modified in the direction of increased selfing with semi-homostylous populations occurring at the margins of their respective Neotropical distributions (Barrett, 1978, 1979, 1985a). Recent work has focussed on *E. paniculata* since populations of this species display a wide spectrum of floral modifications ranging from complete tristily to semi-homostily (Fig. 5). Unlike its tristylous congeners (*E. crassipes* and *E. azurea*) the species does not exhibit extensive clonal propagation, and is a short-lived perennial or annual diploid which regenerates exclusively by seed. These features simplify experimental studies and enable genetic changes to be detected more readily in natural populations.

Eichhornia paniculata has a markedly disjunct distribution, with the major centers of occurrence in N.E. Brazil and the Caribbean (Cuba and Jamaica). Surveys of style morph frequency and studies of the ecological genetics of populations in the two regions have provided useful insights into the breakdown process. Figure 6 illustrates stages in the breakdown of tristily to semi-

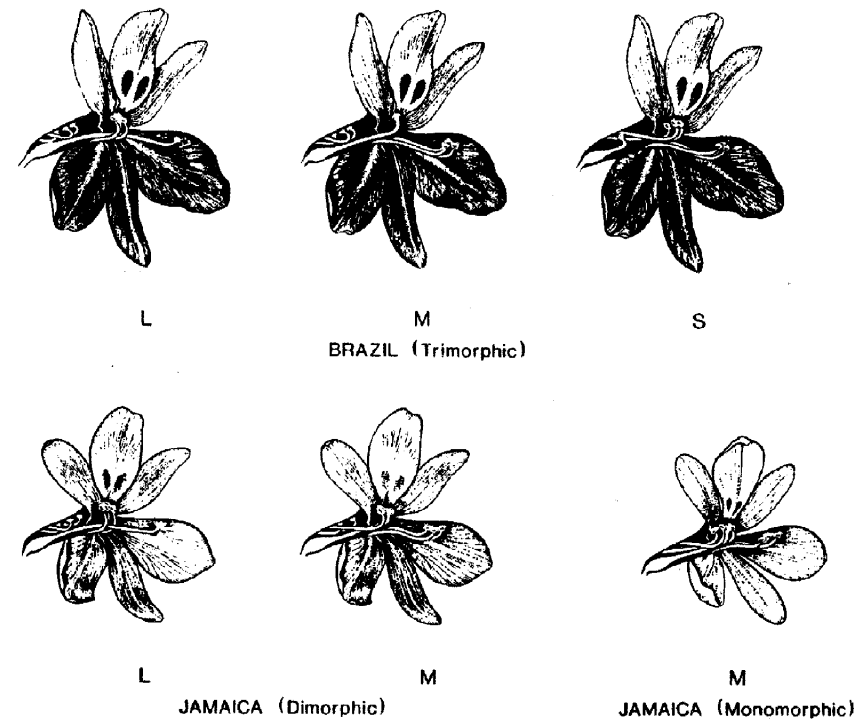


Figure 5. The evolutionary breakdown of tristily to semi-homostily in *Eichhornia paniculata*. The change from outcrossing to selfing is accompanied by a reduction in the size and conspicuousness of flowers. Genetic modifications in stamen position that cause self-pollination occur in the M morph of dimorphic and monomorphic populations.

homostily. The model is based on observations of the patterns of style morph distribution in natural populations and studies of the mating systems and reproductive ecology of populations (Barrett, 1985b; Glover and Barrett, 1986; Barrett et al., 1989). Among populations that we have surveyed in Brazil, 58 were trimorphic, with the S morph under-represented, 21 were dimorphic, composed of the L and M morph, and 5 were fixed for self-pollinating variants of the M morph. On Jamaica the S morph is absent from the island, all plants of the M morph are self-pollinating variants, and the L morph occurs at low frequency in a small number of populations (Fig. 7).

The evolution of selfing in *E. paniculata* involves two key stages. The first involves loss of the S allele, and hence the S

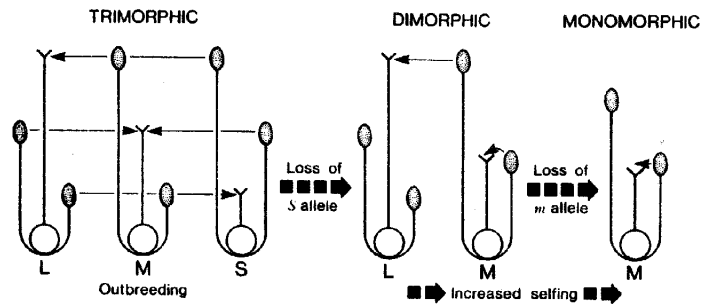


Figure 6. Model of the breakdown of tristily to semi-homostyly in *Eichhornia paniculata*. Arrows indicate the predominant matings. Note modifications in the short-stamen position of the M morph in dimorphis and monomorphic populations. After Barrett (1985b).

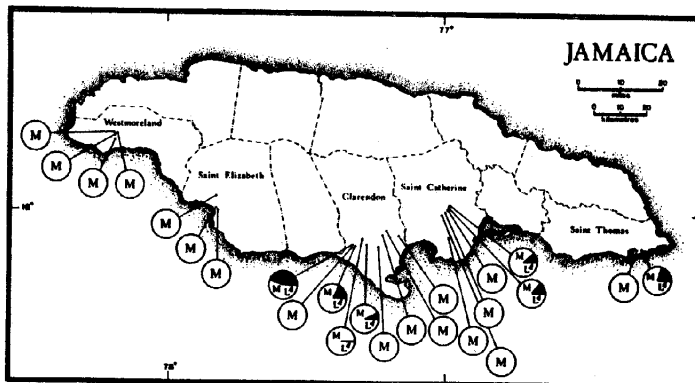


Figure 7. Pattern of style morph distribution in *Eichhornia paniculata* populations from Jamaica. Surveys were conducted in January 1979, 1984, 1987. The figure illustrates all populations that were located during these time periods. All plants of the M morph in Jamaica exhibit modified short stamens. After Barrett, 1988b.

morph; and the second, the loss of the *m* allele and thus the L morph. The most likely explanation for loss of the S morph from populations of *E. paniculata* involves the effect of stochastic influences on population size as a result of bottlenecks and random dispersal. Since the species is highly self-compatible, polymorphic populations can arise from selfing and segregation of genotypes heterozygous at the *S* and *M* loci. Since the dominant *S* allele is carried only by the S morph, separate introductions of this morph are necessary for it to become established in all three morphs and the *M* allele by the M and S morphs. Computer simulation studies by Heuch (1980) on the effects of random fluctuations of population size in tristylous systems confirm that the S morph is most often lost from populations. Survey data of style morph distribution in the related *E. crassipes* indicate a similar pattern, with the S morph absent from many parts of the New World range (Barrett and Forno, 1982), as well as from the entire adventive Old World range (Barrett, 1977). In the latter case, genotypes of the S morph were presumably not represented among the clones transported to the Old World by humans.

Evidence to support the bottleneck hypothesis comes from surveys of the size, density and distribution of *E. paniculata* populations in N.E. Brazil (Barrett et al., 1989). Trimorphic populations are often large in size, dense, and the majority that we have located are concentrated in two major geographical areas. In contrast, dimorphic and monomorphic populations are often composed of a small number of scattered individuals and most are geographically isolated from the main population centers. This pattern suggests that colonizing episodes, perhaps to ecologically marginal sites, have led to loss of the S morph from populations. Studies of the demography and population genetics of tristylous and non-tristylous populations would be valuable in assessing the bottleneck hypothesis.

Two contrasting but not mutually exclusive selective mechanisms can explain the loss of the L morph from populations of *E. paniculata*. The first involves reproductive assurance favoring the M morph, the second automatic selection of the M morph through mating asymmetries between the morphs. Both are initiated by genetic modifications of the M morph which enable it to self-pollinate. These changes appear to be quite widespread in nature as virtually all non-tristylous populations that we have observed contain selfing variants of the M morph. The modifications involve different degrees of elongation of the three filaments of the short-stamen level. The initial step, which is commonly observed in dimorphic populations, involves a single

stamen that elongates to a position equivalent to that of the mid-level stigma (Fig. 6). This results in autonomous self-pollination of the flower. Subsequent modifications, which are largely restricted to monomorphic populations, involve elongation of the two remaining stamens of the short level. These finally take up a position in the mid region of the flower resulting in full semi-homostyly.

Modified M plants of *E. paniculata* rarely occur in tristylous populations and the genes that modify stamen position have no significant phenotypic effects when transferred to the L and S morphs. As a result, in dimorphic populations plants of the M morph frequently display genetic modifications of stamen position, whereas the L morph remains unmodified. This difference has a profound effect on the mating system of populations. Unlike tristylous populations where each morph is highly outcrossed, in dimorphic populations the M morph experiences a high level of self-fertilization whereas the L morph remains largely outcrossing (Fig. 8). With this mating asymmetry among the morphs and no major fitness differences between progeny arising from them, the M morph will replace the L morph. This is because genes that cause an increased rate of self-fertilization have an automatic advantage, since the maternal parent will transmit genes via both pollen and ovules to selfed progeny and thus evade the "cost of meiosis." It should be noted that while we have verified that the maternal outcrossing rates of the L and M morphs are consistent with the model presented in (Fig. 6), we have yet to measure the male fertility of the two morphs to confirm that the M morph has higher male fitness. Experiments with electrophoretic markers similar to those undertaken by Schoen and Clegg (1985) are in progress to enable us to do this. Populations of *E. paniculata* on the island of Jamaica are short-lived as a result of frequent droughts and human disturbance. As a consequence, it seems probable that reproductive assurance may be a more important selective factor in determining the relative frequency of style morphs on the island than the mating asymmetry hypothesis discussed above. The large number of monomorphic M populations on the island (Fig. 7) most likely results from repeated colonizing events and periods of low density. These conditions would favor establishment of self-pollinating variants of the M morph over the non-autogamous L morph. Erratic pollinator service and the absence of specialized long-tongued bees on Jamaica prevent the normal functioning of heterostyly and result in a considerable fertility advantage to the M morph in comparison with the L morph in dimorphic populations (Fig. 9). In contrast, in tristylous populations from

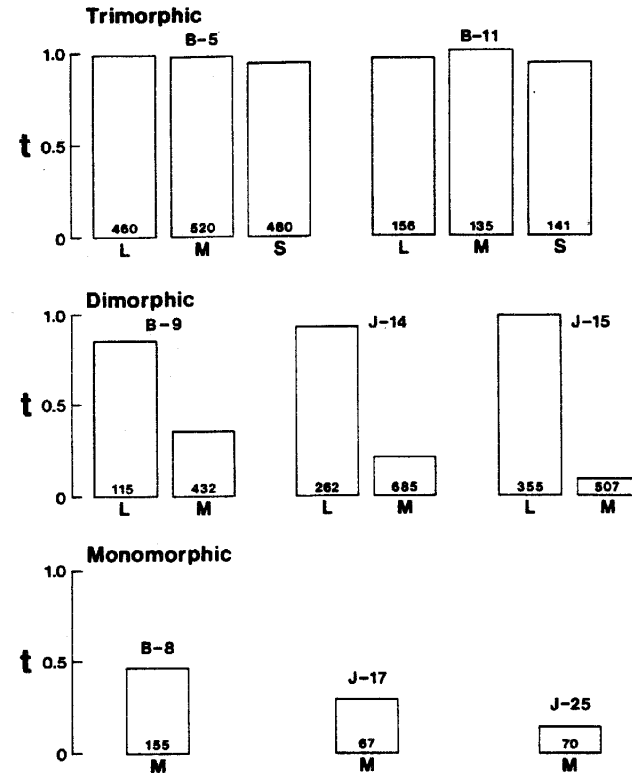


Figure 8. Multilocus estimates of outcrossing rate (t) of the floral morphs in trimorphic, dimorphic and monomorphic populations of *Eichhornia paniculata* from N.E. Brazil (B) and Jamaica (J). Outcrossing rates were estimated by the method of Ritland and Jain (1981) using isozyme loci. The number of progeny assayed per morph are indicated. Within trimorphic populations there were no significant differences between the outcrossing rates of floral morphs whereas in dimorphic populations the morphs differed significantly ($P < 0.001$) in outcrossing rate.

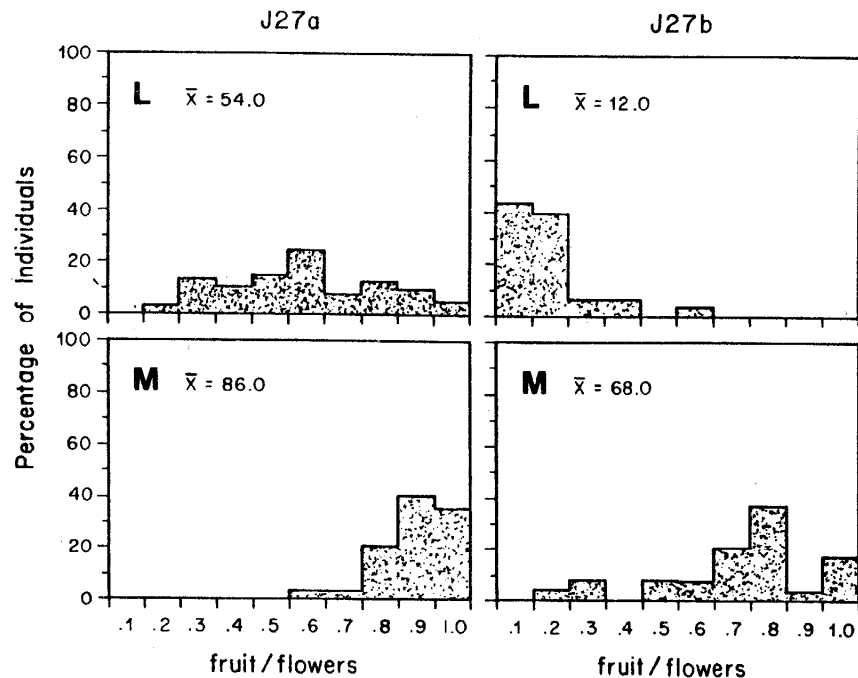


Figure 9. Fruit set of floral morphs in two dimorphic populations of *Eichhornia paniculata* from Jamaica. All plants of the M morph in both populations were selfing variants with a high capacity for autonomous self-pollination. The L morph is non-autogamous because of well-developed herkogamy.

N.E. Brazil specialized pollinators are abundant, fruit set is generally high, and estimates of disassortative mating indicate that most matings occur between the floral morphs (Barrett et al., 1987, 1989)

Investigations of the mating systems and genetic structure of *E. paniculata* populations from N.E. Brazil and Jamaica point to the importance of both founder effects and increased selfing on genetic diversity (Glover and Barrett, 1987; B. C. Husband and S. C. H. Barrett, unpubl. data). A survey of 21 allozyme loci in 11 populations revealed that Jamaican populations were genetically depauperate in comparison with those from Brazil. The low levels of allozyme polymorphism on Jamaica probably result from a restricted number of long-distance dispersal events to the island. The predominance of self-pollinating variants of the M morph on Jamaica suggests that they were favored during establishment after long-distance dispersal. Among the 11 populations surveyed, outcrossing rates were significantly correlated with the

number of polymorphic loci, alleles per locus, observed heterozygosity, and genetic diversity of populations. These results indicate the important influence of both the mating system and founder events on levels of genetic variation in plant populations.

CONCLUSION

Experimental studies on the evolutionary genetics of two ecologically distinct heterostylous groups indicate that the evolution of self-fertilization from outcrossing is associated with colonizing episodes and periods of low population density. The geographical distribution of floral forms in both groups provide evidence in support of Baker's Law. In *Turnera ulmifolia* self-compatible homostyles occur at the margins of the range of the complex and have successfully established on many small islands in the Caribbean where self-incompatible forms are absent. In *Eichhornia paniculata* most populations in N.E. Brazil are tristylous and likely outcrossing, whereas on the island of Jamaica autogamous semi-homostylous variants of the M morph predominate. Although in this species all populations, regardless of floral morphology, are highly self-compatible, the capacity for autonomous self-pollination in homostyles must have provided a selective advantage in establishment and subsequent spread on the island following long-distance dispersal. Baker's Law contrasts the colonizing ability of self-compatible and self-incompatible plants. Self-compatible species populations that are highly autogamous are likely to be favored in establishment after long-distance dispersal.

SUMMARY

The evolution of predominant selfing from obligate outcrossing is one of the major pathways of mating system evolution in flowering plants. Heterostylous genetic polymorphisms (distyly and tristyly) provide a rich source of material in which to test hypotheses concerned with the evolution of self-fertilization. Studies of two Neotropical heterostylous groups (*Turnera ulmifolia* complex and *Eichhornia* spp.) provide evidence that the breakdown of heterostyly to homostyly is associated with colonizing episodes and periods of low population density. The self-pollinating habit of homostyles provides reproductive assurance under conditions of uncertain pollinator service. In *T. ulmifolia* homostyles arise in one step by recombination in the supergene that controls distyly. Crossing studies indicate that this has occurred on at least three occasions in the species complex in association with changes in ploidal level. Selection for increased outcrossing appears to have favored the

evolution of herkogamy in homostylous populations of *T. ulmifolia*. The breakdown of tristily in *Eichhornia paniculata* occurs in distinct stages, with the mating system evolving gradually towards increased levels of self-fertilization. Stochastic influences on population size and the spread of mating system modifier genes result in changes from floral trimorphism through dimorphism to monomorphism. Polymorphic sexual systems, such as heterostyly, provide excellent material for empirical studies of mating system evolution.

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